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Comparative Analysis of Weight Gain, Hand/Wrist Maturation, and Dental Emergence Rates in Chimpanzees Aged 0–24 Months From Varying Captive Environments

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ABSTRACT Variability during the first 2 years of growth and development is examined in captive chimpanzees. The mixed longitudinal study of 175 animals compares curves of weight, hand/wrist maturation, and dental emergence for groups within the sample which differ in sex, rearing circumstances (mother-reared versus hand-reared), and colony (Primate Foundation of Arizona, White Sands Research Center, and The University of Texas M.D. Anderson Cancer Center Department of Veterinary Sciences in Bastrop, Texas). Comparison of LOWESS fits of the curves, using a conservative jackknife approach, reveals trends toward significant differences between colonies for weight (with 4 comparisons reaching significance) and between rearing groups for maturation (1 reaching significance). Results of a full versus reduced model approach show the same trends, for which significance is reached in a higher number of comparisons. The latter approach also indicates possible effects of sex and environmental differences on dental emergence rate. Difficulties with both approaches are discussed. It is concluded that the results are suggestive of significant sex and environmental effects on the variables monitored, justifying further analysis and continuation of the study. The study is significant in 1) providing norms specific to sex and rearing and colony environments with which individual colony animals may be compared in the assessment of their development and in 2) providing a standard, based upon data from a larger and more varied captive chimpanzee population than previously available, with which the dental emergence status and hand/wrist maturation of fossil apes and hominids may be compared.

Prior studies of chimpanzee growth and development have been limited in sample size and/or limited in range of variability, age range over which data were collected, and nature of the data collected. A longitudinal study at Yerkes Laboratories of Primate Biology monitored weight gain, body segment size increase, hand/wrist ossification, and dental emergence for a sample of 16 hand-reared male and female chimpanzees over their full growth period (Grether and Yerkes, 1940; Nissen and Riesen, 1945, 1949, 1964; Gavan, 1953, 1967, 1971; Watts and Gavan, 1982). A comparison of hand/wrist

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ossification data in this group with data for 43 additional animals, raised in different circumstances at the Yerkes Laboratories, revealed some evidence of environmental and physiological factors that might affect the rate of ossification (Nissen and Riesen, 1949). A second study, begun in 1980 at the Primate Research Institute, Holloman AFB, New Mexico (Lawrence and Gorzitze, 1985), followed weight gain in 62 hand-reared male and female infants from birth to 1 year. Uehara and Nishida (1986) weighed 19 wild male and female chimpanzees over a 7-year period from 1973 to 1980. More recently, a retrospective investigation was made of dental emergence records at the Laboratory for Experimental Medicine and Surgery in Primates (LEMSIP) for 58 males and females, apparently of mixed rearing history (Conroy and Mahoney, 1991; Kuykendall et al., 1992).

This study examines the magnitude of variability in captive chimpanzee growth and development. The question is important for two reasons. First, there is a need for data on norms and range of variability with which to compare individual animals in assessing their development. This is fundamental to good colony management. Second, the determination of developmental stages in fossil hominid species depends upon data on norms and variability in living species used as models for the interpretation of fossils.

The study, which was initiated 13 years ago at the Primate Foundation of Arizona, monitors weight gain, dental emergence, hand/wrist maturation, and body segment size increase in a large, mixed longitudinal sample of chimpanzees of both sexes, some hand-reared and others reared for at least 1 year by their mothers, at three captive colonies (Hawkey et al., 1989; Marzke et al., 1987, 1989, 1993). Variability is examined both across the full sample and among groups within the sample classified by sex, rearing history, and colony.

Since the collection of data has been opportunistic, the sample contains varying numbers of animals at each age and varying numbers of data points for each animal. This is a problem common to many growth and development studies of nonhuman primates, which complicates the comparative analysis of growth curves. We have explored two approaches to the comparative analysis of our growth curves, and report here on what we have found to be the relative advantages and disadvantages of each. Comparison of results from the two analyses reveals trends which we suspect will be confirmed as our sample size increases. It is hoped that our report of results from these two pilot attempts to draw meaningful inferences from data like ours will generate interest in the development of more sophisticated models for analysis of such data.

The study is still in progress, and covers the full range of growth and development from birth to over 12 years of age. The results reported here are restricted to the analysis of data on weight gain, dental emergence, and maturation over the first 24 months.

MATERIALS AND METHODS

Sample

A total of 175 chimpanzees is included in the present analysis. All were free of chronic illness(es). For the purpose of our comparative analysis of curves for weight, hand/wrist maturation, and dental emergence, they are categorized into groups distinguished on the basis of colony in which they live, their rearing status (raised by hand or with their mothers), and sex. The animals are from three captive colonies: The Primate Foundation of Arizona (PFA), the White Sands Research Center (WS), and The University of Texas M.D. Anderson Cancer Center Department of Veterinary Sciences in Bastrop, Texas (BA). The rearing/sex combinations in the categories include hand-reared females (HF), hand-reared males (HM), mother-reared females (MF) and mother-reared males (MM). An animal is categorized as mother-reared if it has spent at least 12 months with its mother. All BA animals in this category were with their mothers for the full 24 months covered here. Twelve of the PFA mother-reared animals were separated between the ages of 12 and 24 months (at mean ages of 12.8 months for females and 15 months for males). The PFA mother-reared sample is more variable in its composition than the BA sample, probably because eight

TABLE 1. Weight analysis: Number of data points, number of animals, age range, and LOWESS results for R^2 and mean square error, by colony and rearing/sex group

Group	N data points	N animals	Age range (months)	R^2	MSE
PFA HF	62	10	0–24	.93	.612
PFA HM	20	6	6–24	.67	1.335
PFA MF	29	11	1–24	.71	1.104
PFA MM	52	17	3–24	.71	1.157
WS HF	196	28	0–24	.93	.488
WS HM	118	24	1–24	.90	.644
BA HF	101	21	0–24	.85	.922
BA HM	98	13	0–24	.92	.688
BA MF	84	24	0–24	.91	.599
BA MM	80	21	0–24	.86	.783
All groups	840	175	0–24	.82	.935

TABLE 2. Hand/wrist maturation analysis: Number of data points, number of animals, age range, and LOWESS results for R^2 and mean square error, by colony and rearing/sex category

Group	N data points	N animals	Age range (months)	R^2	MSE
PFA HF	23	9	0–22	.67	72.97
PFA HM	16	6	6–24	.71	64.51
PFA MF	18	10	12–24	.42	93.51
PFA MM	37	17	5–24	.22	91.34
WS HF	161	27	0–24	.79	40.34
WS HM	112	24	1–24	.76	36.69
All groups	386	110	0–24	.62	61.48

TABLE 3. Dental emergence analysis: Number of data points, number of animals, and LOWESS results for R^2 and mean square error, by colony and rearing/sex category

Group	N data points	N animals	Age range (months)	R^2	MSE
PFA HF	76	11	0.5–24	.91	1.02
PFA HM	38	6	2–24	.83	1.37
PFA MF	47	13	0.5–24	.82	1.49
PFA MM	56	17	3–24	.79	1.00
WS HF	189	27	0–24	.90	1.07
WS HM	131	25	1–24	.89	1.07
BA HF	23	14	3–24	.76	1.73
BA HM	16	7	2–23	.79	1.55
BA MF	80	25	0–24	.87	1.27
BA MM	63	24	2–24	.88	.948
All groups	719	169	0–24	.87	1.17

of the animals were born at another institution, where they had a different routine and spent varying amounts of time before reaching PFA. Sizes of the colony/rearing/sex groups are shown in Tables 1–3. The sizes vary according to the growth variable for which the groups are compared.

Most of the animals have been observed more than once, and many have been observed twice per year over a long period of time. Thus there are considerably more data points than animals (Tables 1–3). It should be noted that data are available only for HM and HF at WS, and that there are not sufficient hand/wrist maturation data from BA for use in group comparisons at this time. However, the BA maturation data for 17 animals (19 data points) are included in the "All groups" sample for Table 2 and Figure 4.

Environments

The hand-rearing protocols and nutritional, physical, and social environments vary among the three chimpanzee colonies.

Although all hand-reared chimpanzee infants were fed with formulas for human infants, no attempt was made in this study to compare the different feeding regimens, because these varied not only between colonies, but also within individual colonies over the years in which data were collected.

At PFA the animals were housed inside in small social groups of varying combinations during the early stages of the study. More recently they have had access to outdoor cages as well. At BA, the animals form larger social groups of adult males and females, juveniles, and infants in large outdoor corrals during the day. Hand-reared animals at all three colonies have contact with both colony personnel and their peers.

Data collection

Data are collected when the chimpanzees are anaesthetized during routine health examinations. Posterior-anterior radiographs of the hands are obtained with the hands taped flat onto the cassettes. A maturation score is assigned to each radiograph, using a modified Tanner-Whitehouse system (Tanner et al., 1983). This score reflects the overall stage of ossification of the wrist and hand centers. Teeth are recorded as erupted if any part of the enamel is exposed beyond the gum.

Statistical analysis

Growth curves were fitted to the data using the LOWESS method for estimating the growth response for each age (Cleveland, 1979). LOWESS stands for "locally weighted regression scatterplot smoothing." It uses fitting of locally linear or polynomial functions to estimate the true growth curve. The LOWESS method was used to fit curves to the present data since the relationship of the responses over the age range considered here does not consistently conform to a linear regression or other known growth model. The LOWESS method has been successfully used in modelling baboon growth in Moses et al. (1992). The window (f = fraction of data) used in constructing the estimated curve at each point was selected by the M plot method of Cleveland and Devlin (1988), which is an extension of the Mallows C_p criterion for model selection in multiple linear regression. In the vast majority of the fits, the M plot method selected a value of $f = 1.00$. In order to compare the various LOWESS fits it was decided to use $f = 1.00$ for all fits. The degree of the local fitting polynomial was taken to be one (i.e., local linear fitting) for the weight and maturation data. Local quadratic fitting (degree = 2) was used for the dental data due to the initial rise and then leveling off of the total number of teeth over the two year age span considered here.

Two methods were explored for comparing growth curves of different colony, rearing, and sex groups. The first is the jackknife method of comparing areas under growth curves used in Moses et al. (1992). This method effectively deals with the problem of multiple measurements on each animal and the associated correlations among such measurements by jackknifing on each animal. Each animal in turn is left out of the data set and the area under the LOWESS fit is found. This gives an estimated mean area under the growth curve and a measure of the variance of this area. Unfortunately there are two drawbacks. The first is that two growth curves can have the same areas under them and not be the same. The second is that the age range over which the growth characteristic of the two groups could be compared had to be restricted so that there were at least two animals at the minimum and maximum ages in the range. If there is only one animal at an endpoint, the area under the LOWESS fit when this animal is left out will tend to be smaller than what would be expected since the age range is smaller. This will lead to an inflation in the variance of the areas and lead to a less powerful test. Also the small number of animals in some age groups limits the number of comparisons that can be made with the jackknife method. (See, for example, the age ranges in Table 4 for comparison of BA with WS and with PFA in weight).

The second method is a full versus reduced model approach involving the fitted LOWESS curves. (See Neter et al., 1990, for a discussion of the full versus reduced model approach to hypothesis testing in multiple linear regression.) This method of comparing fits is similar to the standard method for

TABLE 4. Results of jacknife comparison of LOWESS curves for weight among colonies and rearing/sex groups

Comparison	Group 1	Group 2	Min. usable age	Max. usable age	Group 1 No. of animals	Group 1 No. of data points	Group 2 No. of animals	Group 2 No. of data points	Z stat	*P* value based on Z
Colonies	BA HF	PFA HF	0	21	21	100	10	54	0.592	0.5538
	BA HF	WS HF	0	21	21	100	28	187	0.5165	0.6055
*	BA HM	PFA HM	10	14	6	10	5	6	3.6424	0.0003
	BA HM	WS HM	1	24	12	86	24	118	1.8857	0.0593
	BA MF	PFA MF	12	24	22	39	10	23	2.1249	0.0336
	BA MM	PFA MM	6	24	21	62	17	48	1.9368	0.0528
	PFA HF	WS HF	0	23	10	61	28	194	0.3435	0.7312
*	PFA HM	WS HM	10	14	5	6	17	29	−3.2298	0.0012
Rearing groups	BA HF	BA MF	0	21	21	100	25	77	1.9528	0.0508
*	BA HM	BA MM	0	24	13	98	23	80	4.9283	0
*	PFA HF	PFA MF	12	23	9	30	9	20	3.6905	0.0002
	PFA HM	PFA MM	14	19	6	9	12	20	1.6891	0.0912
Sexes	BA HF	BA HM	0	14	21	91	13	87	−1.3492	0.1773
	BA MF	BA MM	0	24	25	84	23	80	−0.7	0.4839
	PFA HF	PFA HM	10	19	7	22	6	13	1.146	0.2518
	PFA MF	PFA MM	12	24	10	23	16	42	−0.9541	0.3401
	WS HF	WS HM	1	24	28	194	24	118	−1.3305	0.1835

* Significant (overall α = .10; individual α level using Bonferroni's method = .10/17 = .0059).

comparing two simple linear regression lines (Neter et al., 1990). The distributions of the sum of squares used to determine the *F* test statistic of equality of growth curves are approximated by the methods given in Cleveland and Devlin (1988). This method has the advantage of comparing the fits directly, as opposed to comparing areas under curves. It also is less restrictive in terms of the age range requirement in that there only needs to be at least one animal at each endpoint of the range. Unfortunately this method treats each data point as an independent measurement. This is not the case since multiple measurements are made on each animal. This correlation may result in a higher chance of rejecting equality of curves when they are actually equal.

The jackknife method is more conservative than the full versus reduced model *F* test approach. The latter approach results in four times as many statistically significant differences between pairs of curves as the jackknife approach, if the overall alpha level is set at 0.10 and Bonferroni's method is used to obtain the individual alphas in the jackknife analysis. (Individual alpha values for a collection of comparisons are set at 0.10/no. of pairs tested for equality.) It was decided to present tables in the text showing only the more conservative results of the jackknife comparison (Tables 4–6). However, a table with results of the full versus reduced analysis is provided in the appendix, and in the discussion section we conjecture about the common trends indicated by the two analyses.

LOWESS fits and their comparisons were obtained by using modifications of macros written in SAS by Friendly (1991). All plots were obtained from SAS/GRAPH (SAS Institute, 1990).

Ages for which pairs of curves were compared by the full versus reduced model approach range from the maximum of the lowest ages for the pair of groups to the minimum of the highest ages. (See Tables 1–3 for the low and high limits of age range for each group).

RESULTS

Weight

Weight versus age overall. The LOWESS fit of weight gain relative to age for all animals in the sample is given in Table 1 and is shown with a 95% prediction band in Figure 1. The relationship is approximately linear during the first 2 years, with a slightly perceptible lowering of the slope beginning at 12 months. The breadth of 95% prediction bands varies among the colony/rearing/sex groups compared, in part because of differences between these groups in sample size

TABLE 5. Results of jacknife comparison of LOWESS curves for maturation among colonies and rearing/sex groups

Comparison	Group 1	Group 2	Min. usable age	Max. usable age	Group 1 No. of animals	Group 1 No. of data points	Group 2 No. of animals	Group 2 No. of data points	Z stat	*P* value based on Z
Colonies	PFA HF	WS HF	11	22	8	18	22	57	1.3635	0.1729
	PFA HM	WS HM	10	14	4	5	16	27	1.6488	0.0992
Rearing groups	PFA HF	PFA MF	17	22	7	11	7	9	1.2694	0.2044
Sexes	PFA HF	PFA HM	14	19	7	8	6	9	1.0743	0.2428
	PFA MF	PFA MM	15	24	10	16	16	29	1.2864	0.2006
*	WS HF	WS HM	1	22	27	156	24	110	2.4211	0.0155

*Significant (overall $\alpha = .10$; individual α level using Bonferroni's method = .10/6 = .0167).

TABLE 6. Results of jackknife comparison of LOWESS curves for tooth emergence among colonies and rearing/sex groups[1]

Comparison	*Group 1*	*Group 2*	Min. usable age	Max. usable age	Group 1 No. of animals	Group 1 No. of data points	Group 2 No. of animals	Group 2 No. of data points	Z stat	*P* value based on Z
Colonies	BA HF	PFA HF	5	21	11	20	11	53	−0.6548	0.5126
	BA HF	WS HF	5	21	11	20	27	136	−0.8374	0.4024
	BA HM	PFA HM	3	8	2	6	4	14	1.383	0.1667
	BA HM	WS HM	3	8	2	6	19	55	1.2276	0.2195
	BA MF	PFA MF	3	23	23	71	12	45	1.3312	0.1832
	BA MM	PFA MM	3	24	23	61	17	56	−0.3083	0.7579
	PFA HF	WS HF	3	23	11	71	27	168	−0.5173	0.605
	PFA HM	WS HM	3	14	5	25	23	91	−0.2857	0.7751
Rearing groups	BA HF	BA MF	5	21	11	20	22	55	−0.3747	0.7079
	BA HM	BA MM	3	8	2	6	13	18	0.8342	0.4042
	PFA HF	PFA MF	3	23	11	71	12	45	1.7005	0.0891
	PFA HM	PFA MM	3	19	6	32	14	39	0.7923	0.4282
Sexes	BA MF	BA MM	3	24	24	73	23	61	−1.2992	0.1939
	PFA HF	PFA HM	3	19	10	57	6	32	0.5463	0.5849
	PFA MF	PFA MM	3	23	12	45	16	51	−2.1617	0.0306
	WS HF	WS HM	1	24	27	187	25	131	0.4492	0.6533

[1]Overall $\alpha = .10$; individual α level using Bonferroni's method = .10/16= .0063.

and in age ranges over which they can be compared.

Colony differences. Significant differences between PFA and BA (Fig. 2) and between PFA and WS are found for hand-reared males (Table 4). It should be noted, however, that the age ranges for comparison by the jackknife method are severely restricted. Clear trends toward differences between hand-reared males of BA and WS, and between mother-reared males and females of BA and PFA are also seen. Males and females of both rearing categories at BA tend to be heavier than their PFA counterparts. The BA hand-reared animals of both sexes also tend to be heavier than those at WS. PFA hand-reared females are heavier than WS females, whereas the reverse is the case for hand-reared males.

Rearing differences. BA hand-reared males are significantly heavier than males raised with their mothers, and PFA hand-reared females are significantly heavier than their mother-raised peers (Table 4; Fig. 3). BA hand-reared females tend to be heavier than the mother-reared, although the difference is not significant.

Sex differences. No statistically significant differences between categories are found for weight. Mean body weights of females and males for each age in months are given in Tables 7 and 8.

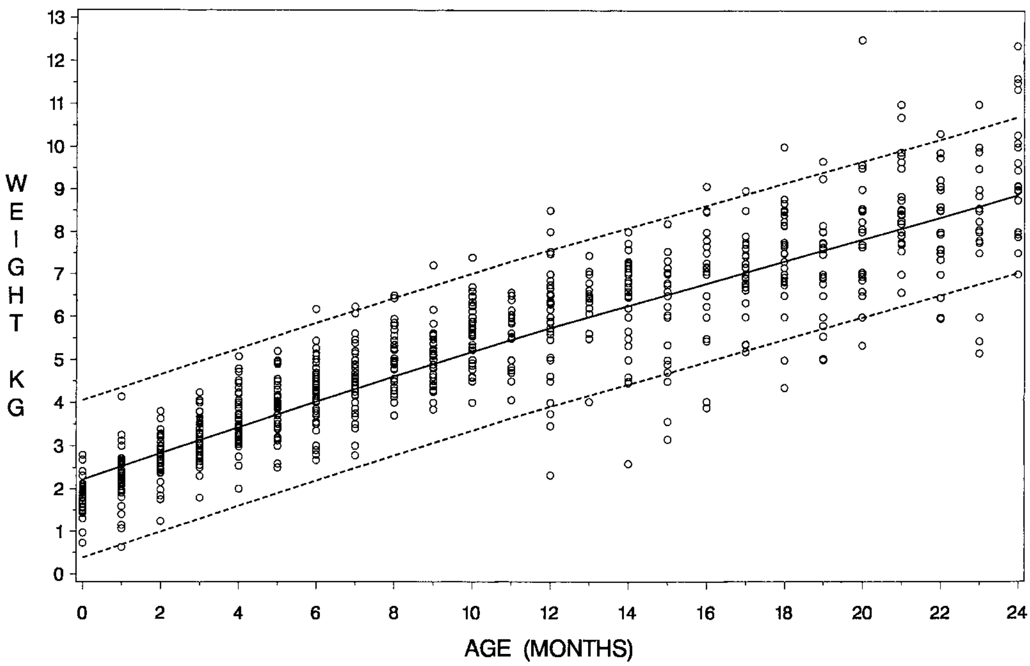

Fig. 1. Weight versus age for the full sample. LOWESS fit and 95% prediction band.

Hand/wrist maturation

Maturation versus age overall. The LOWESS results are given in Table 2. Maturation relative to age (Fig. 4) is approximately linear for the total sample during the first 2 years, although a slight increase in slope is perceptible at about 12 months. (Recall that BA maturation data for 17 animals are included in Table 2 only for the "All groups" sample.)

Colony differences. In the only colony comparisons that can be made with our available data (PFA versus WS hand-reared females and males), maturation is more rapid in the PFA animals, but the differences are not significant (Table 5).

Rearing differences. Rearing comparisons are restricted to data from PFA. For females, the hand-reared animals tend to mature more rapidly than the mother-reared, but the difference is not significant (Table 5).

Sex differences. Hand-reared females mature significantly more rapidly than males at WS (Table 5; Fig. 5).

Mean maturation scores of females and males for each age in months are given in Tables 7 and 8.

Dental emergence

Tooth emergence versus age overall. The LOWESS results are given in Table 3. Tooth emergence is relatively rapid during the first year and slows in the second (Fig. 6).

Colony differences. There are no significant differences among colonies (Table 6).

Rearing differences. There are no significant differences among rearing groups (Table 6).

Sex differences. There are no significant differences, but a clear trend is observed toward earlier tooth emergence in male mother-reared PFA animals, compared with their female counterparts (Table 6; Fig. 7).

Mean dental emergence scores of females

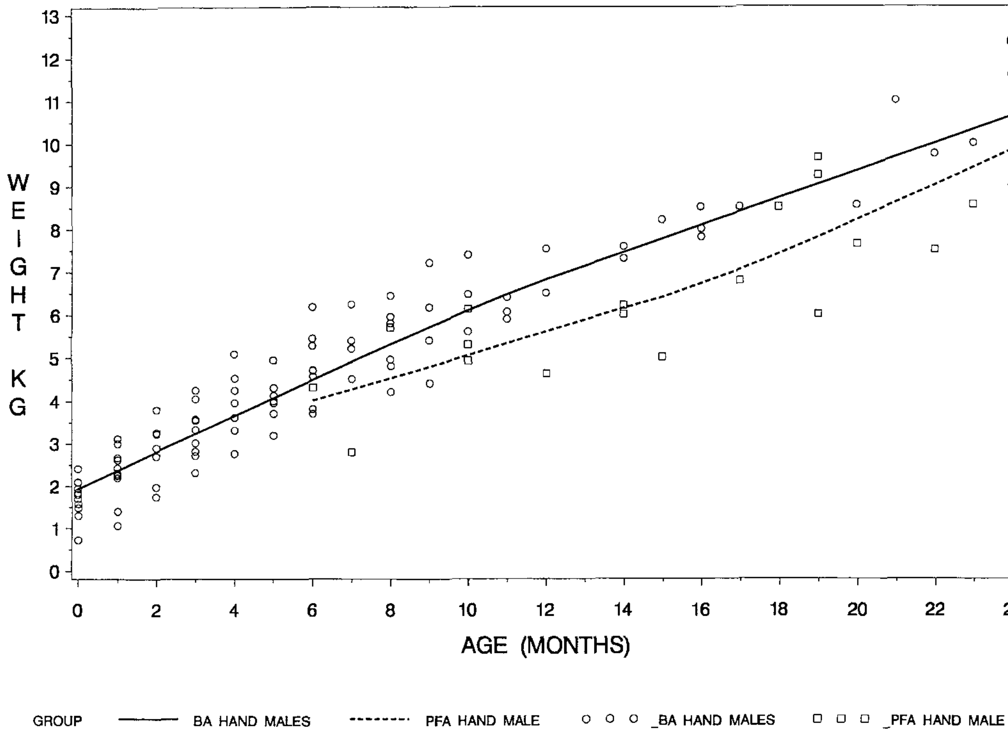

Fig. 2. Comparison of LOWESS fits of colonies in weight versus age: BA and PFA hand-reared males.

and males for each age in months are given in Tables 7 and 8.

Tooth emergence sequence. The sequence of tooth emergence is i1, i2, m1, m2, c. This is the same as the sequence which has been reported by Nissen and Riesen (1945) and by Conroy and Mahoney (1991). Central incisor emergence is the most stable and canine and second deciduous molars are the most variable in our sample (particularly the upper canine in hand-reared males). We have found no clear differences in the sequence of tooth loss.

A longitudinal analysis of 26 animals, for which we have repeated observations and a continuous record of tooth emergence, indicates that there may be at least one sequence polymorphism. In three of these animals, the upper second molar erupted after both canines had emerged. The emergence time for these teeth fell well within 1 standard deviation from the mean emergence for our sample. This deviation pattern has also been reported for 5 chimpanzees by Nissen and Riesen (1945).

In another three animals, the upper second incisor was delayed, erupting after both the first molars in one instance and after both second molars in 2 more animals. Since incisor emergence in these instances lagged considerably behind the average expected emergence time, we are inclined to the view that it is more vulnerable than the other deciduous teeth to environmental factors.

DISCUSSION

The conservative jackknife comparisons of curves for groups within our sample show that environment, rearing, and sex may be significant factors in some aspects of chimpanzee growth and development. Weight gain rates vary significantly between colonies for hand-reared males (PFA versus BA and WS) and between rearing groups for males at BA and for females at PFA. Maturation varies significantly between sexes for

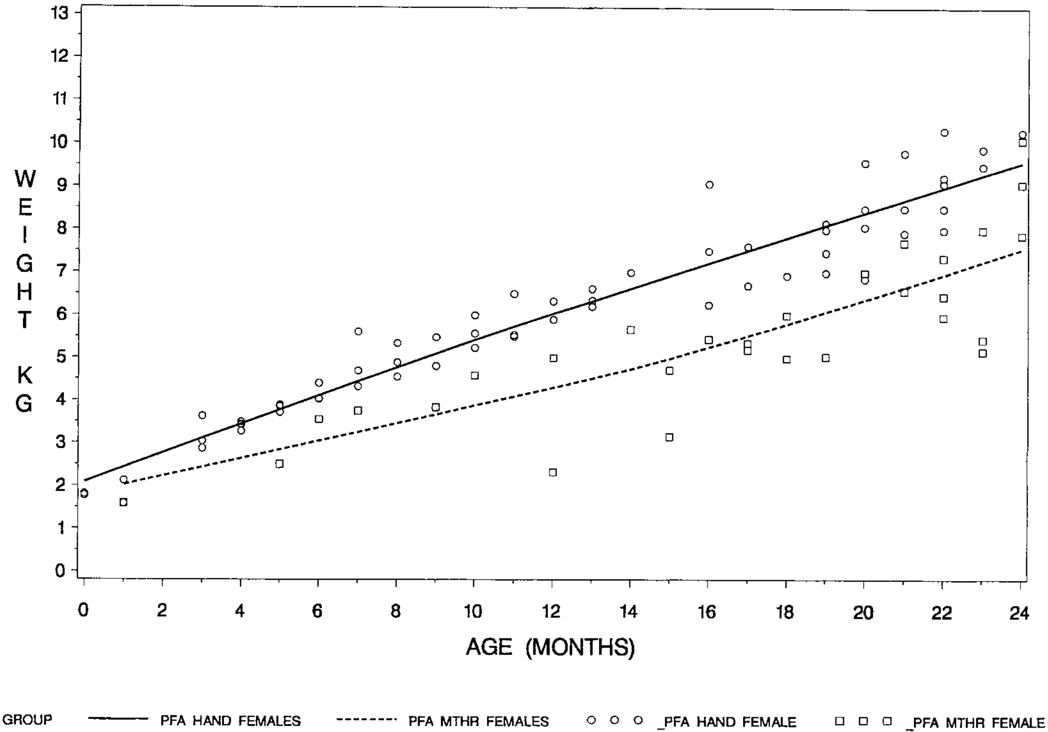

Fig. 3. Comparison of LOWESS fits of rearing groups in weight versus age: PFA hand-reared and mother-reared females.

hand-reared animals at WS. Trends toward significant differences between colonies are seen in mother-reared male and female weights, and also between WS and BA in hand-reared male weights. The difference in dental emergence between sexes in PFA mother-reared animals also approaches significance.

Results of the full versus reduced model analysis of the data (Appendix) show significant differences between four of the five groups for which significant differences were found with the jackknife method, and they approach significance for the fifth (PFA versus WS hand-reared males). They also show significant differences between three groups for which the jackknife method reveals trends (BA HM versus both PFA and WS HM weights, and PFA MF versus PFA MM tooth emergence). Finally, they reveal additional colony and rearing group variability, with significant differences between hand-reared PFA and WS females for hand/wrist maturation, and between female PFA rearing groups for tooth emergence.

The similar patterns in variability of growth and development variables revealed by the two analyses are discussed below, along with their possible implications.

Weight

There is strong evidence in the extent of variability among our colonies and rearing groups that differences in physical and social environment and in nutrition are likely to affect weight gain. There is also a possibility that overall skeletal size may be a factor in the weight differences among colonies. This possibility will be investigated in an analysis of relationships among our weight and body segment size data.

The evidence for effects of rearing and colony differences on weight gain is reinforced by the results of previous studies. Hand-reared chimpanzees at the Yerkes Laboratories of Primate Biology tend to be ahead

TABLE 7. Mean monthly body weights, maturation scores, and number of teeth erupted: Females

Age in months	Mean weight (kg)	S.D.	Min.	Max.	N	Mean maturation score	S.D.	Min.	Max.	N	Mean number of teeth	S.D.	Min.	Max.	N
0	1.87	0.39	0.97	2.79	24	120.5	6.36	116	125	2	0	0	0	0	3
1	2.1	0.52	0.63	2.72	23	130.83	6.01	122	139	6	0	0	0	0	11
2	2.69	0.5	1.24	3.63	23	139.8	14.27	122	171	10	0.36	1.08	0	4	14
3	3.21	0.49	1.79	4.06	29	169.6	33.03	128	224	10	1.54	1.44	0	5	24
4	3.47	0.59	2	4.79	31	161.46	28.24	122	219	13	2.97	1.87	0	6	32
5	3.77	0.72	2.5	5.2	28	175	32.66	142	245	12	3.61	1.91	0	6	31
6	4.01	0.52	2.9	5.01	28	191.92	39.72	144	262	13	5.63	1.1	3	8	30
7	4.42	0.73	3	6.08	22	211.38	28.31	164	251	8	6.33	1.08	5	10	18
8	4.8	0.57	3.69	5.86	21	222.7	40.67	154	276	10	6.4	0.68	5	8	20
9	4.82	0.54	3.84	5.62	21	219.5	42.82	170	320	12	7.21	1.03	6	9	19
10	5.15	0.68	4	6.28	27	246.09	47.95	188	353	11	7.52	1.36	6	10	21
11	5.45	0.62	4.5	6.5	17	285.14	66.61	203	410	7	7.78	0.73	6	9	18
12	5.81	1.35	2.32	8.5	20	212.88	56.59	97	279	8	8.06	1.6	3	10	17
13	6.45	0.44	5.49	7.07	9	295	32.65	237	314	5	9.33	0.87	8	10	9
14	6.48	0.88	5	8	17	279.3	57.46	210	375	10	8.94	1.57	4	10	16
15	6.12	1.35	3.15	7.54	10	266.4	70.5	168	362	5	8.7	1.57	5	10	10
16	6.83	1.12	5.44	9.07	10	355	80.12	282	486	5	9.33	0.87	8	10	9
17	6.94	0.8	5.19	7.75	17	322.64	60.83	216	443	14	9.74	0.56	8	10	19
18	7.28	1.19	4.99	10	16	357.71	55.35	267	435	7	9.75	0.62	8	10	12
19	7.25	0.88	5.03	8.15	11	372.67	93.61	283	547	6	10	0	10	10	12
20	8.25	1.5	6.5	12.5	16	415.13	75.09	288	550	8	9.88	0.33	9	10	17
21	8.39	1.06	6.58	10.7	18	376.38	75.25	300	528	8	10	0	10	10	16
22	8.16	1.18	5.97	10.32	13	397.78	99.02	242	562	9	10	0	10	10	13
23	7.87	1.45	5.16	9.89	23	401.2	127.47	189	506	5	10	0	10	10	14
24	9.2	1.26	7	11.5	24	426.75	57.89	350	481	4	10	0	10	10	7

TABLE 8. Mean monthly body weights, maturation scores, and number of teeth erupted: Males

Age in months	Mean weight (kg)	S.D.	Min.	Max.	N	Mean maturation score	S.D.	Min.	Max.	N	Mean number of teeth	S.D.	Min.	Max.	N
0	1.71	0.39	0.73	2.41	17	122	1.419	121	123	2	0	0	0	0	1
1	2.48	0.69	1.07	4.14	18	135	3	132	138	3	0	0	0	0	3
2	2.83	0.52	1.75	3.8	18	144.63	22.81	123	192	8	0.25	0.45	0	1	12
3	3.26	0.51	2.3	4.24	20	145.5	12.19	131	164	6	2.39	1.75	0	6	18
4	3.65	0.56	2.75	5.08	22	142	9.42	127	157	11	3.26	1.85	0	6	19
5	3.87	0.56	2.59	4.94	19	172	29.05	145	244	10	4.18	1.74	1	6	17
6	4.36	0.84	2.67	6.18	22	156.17	335.97	132	225	6	5.44	1.46	2	7	16
7	4.53	0.86	2.78	6.24	18	194.11	38.15	155	277	9	5.83	0.79	3	7	18
8	5.26	0.8	4.14	6.5	14	175.56	24.45	151	222	9	6.71	1.26	4	8	17
9	5.31	0.82	4.4	7.21	12	189.25	35.59	151	237	4	6.6	0.84	6	8	10
10	5.8	0.83	4	7.39	21	213.86	44.51	154	285	14	7.71	1.1	6	10	17
11	5.31	0.9	4.06	6.57	10	221.5	52.81	158	272	6	8.13	1.13	6	10	8
12	5.77	1.27	3.46	7.53	15	222.7	43.5	145	280	10	8	0.88	6	10	14
13	5.95	1.06	4.02	7.44	8	225.75	44.87	189	291	4	8.78	0.83	8	10	9
14	5.89	1.55	2.59	7.73	13	244	40.3	201	312	7	8.81	1.28	6	10	16
15	6.27	1.33	3.56	8.2	15	293.44	54.45	210	390	9	9.06	1	8	10	16
16	6.62	1.59	3.88	8.5	12	244	171.12	123	365	2	9.29	0.76	8	10	7
17	7.2	1.05	5.37	8.97	10	253	63.51	135	354	10	9.5	0.85	8	10	10
18	7.3	1.14	4.35	8.77	17	284.09	68.83	135	408	11	9.82	0.53	8	10	17
19	6.91	1.51	5	9.66	11	313.38	131.95	129	444	8	9.75	0.62	8	10	12
20	7.17	1.03	5.34	8.55	9	284	81.91	152	376	5	10	0	10	10	7
21	8.67	1.09	7	11	9	356.6	49.17	273	398	5	10	0	10	10	10
22	8.14	1.15	6	9.87	12	293.5	108.11	158	423	6	10	0	10	10	10
23	8.61	1.32	6	11	11	316.67	78.31	164	370	6	10	0	10	10	8
24	9.44	1.43	7.5	12.36	15	420	87.65	275	542	7	10	0	10	10	12

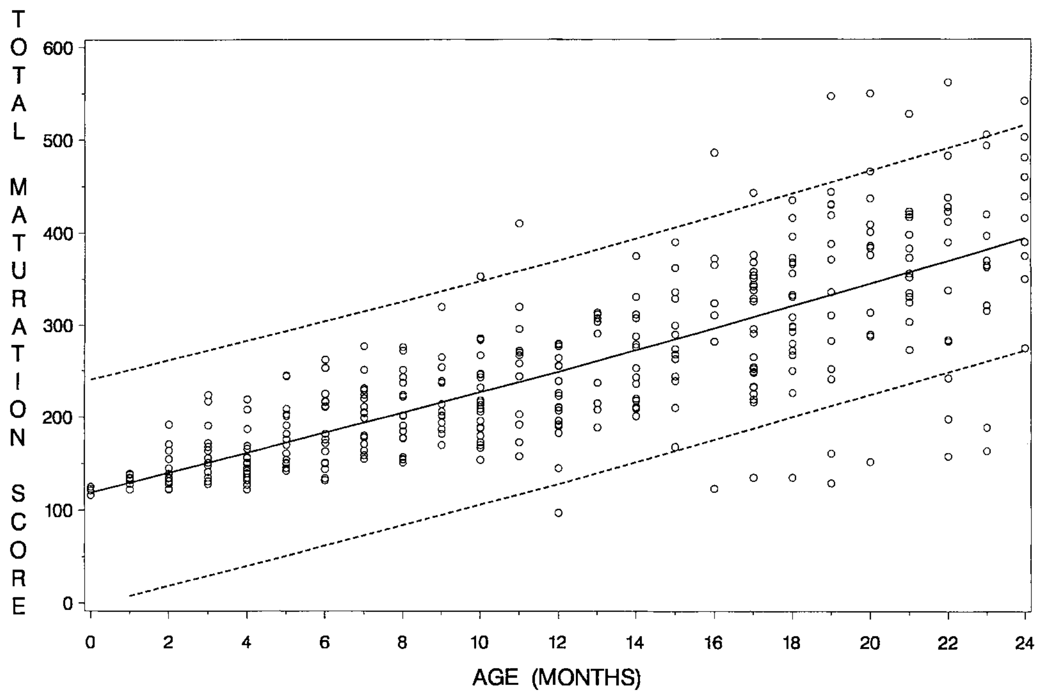

Fig. 4. Maturation score versus age for the full sample. LOWESS fit and 95% prediction band.

of mother-reared ones during their first year (Nissen and Riesen, 1945), and the hand-reared animals at both Yerkes Laboratories (Gavan, 1971) and the Primate Research Institute (Lawrence and Gorzitze, 1985) appear to be heavier on the average, over the 0–24 month age range, than the animals in our sample (Marzke et al., in press).

Neither of our analyses, nor those of Gavan (1971) and of Lawrence and Gorzitze (1985) indicates a clear and consistent effect of sex on weight gain.

Hand/wrist maturation

Sex does appear to be a factor in hand/wrist maturation. A significant difference between WS hand-reared males and females is shown by both of our analyses. It is suspected that the smaller PFA sample sizes may explain the lack of significance in the difference between PFA hand-reared males and females shown by the jackknife analysis. The tendency for females to be advanced over males in maturation during the first 2 years is consistent enough across colonies and rearing groups to suggest that hand/wrist maturation is likely to be affected by the sex of an individual regardless of the circumstances under which it is raised.

Differences among the four groups of animals in maturation rate may relate in part to differences in the ways, or in the extent to which, they use their hands. We are led to this supposition by evidence that ossification in our chimpanzees occurs early in the more proximal regions of the hand and wrist stressed in knuckle-walking, whereas in humans the more peripheral phalanges ossify relatively earlier (Marzke et al., 1987). A similar observation was made by Nissen and Riesen (1949). It therefore looks as if stresses associated with uses of the hand may play a role in timing of ossification. If this is the case, an explanation for differences among colony/rearing/sex groups of chimpanzees in ossification rate may be sought by comparing the groups in the amount and nature of locomotion during hand/wrist maturation.

Dental emergence

Tooth emergence appears to be less affected by the factors of sex, rearing, and envi-

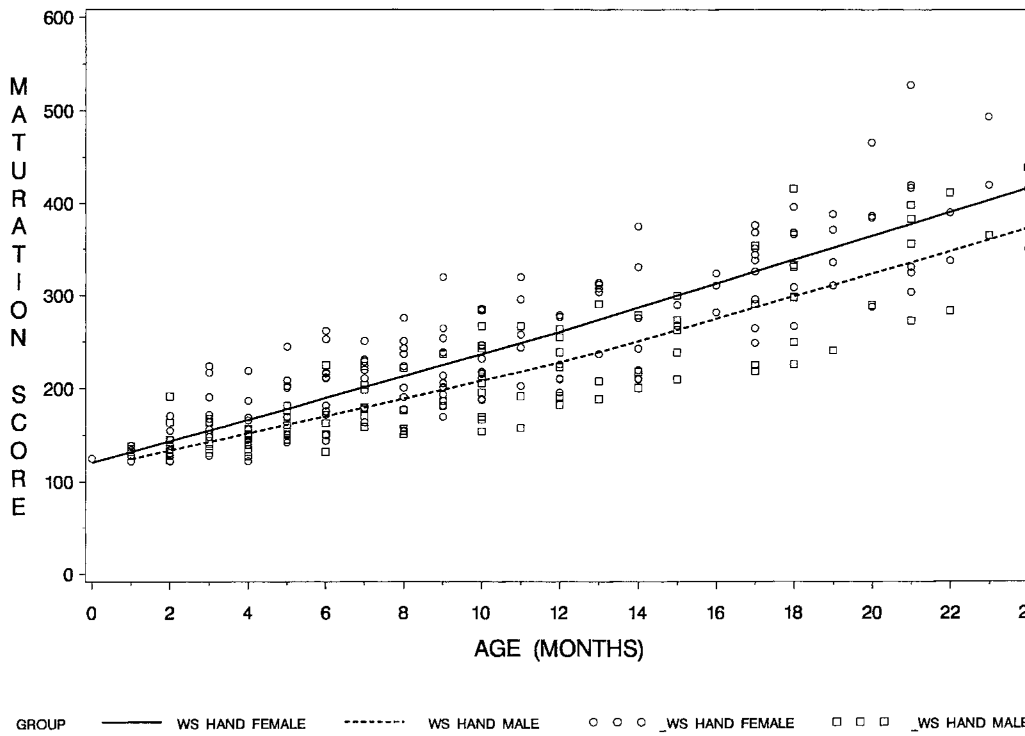

Fig. 5. Comparison of sexes in maturation score versus age: WS hand-reared females and males. Comparison of LOWESS fits.

ronment than are weight gain and hand/wrist maturation. The lack of evidence in our jackknife analysis for a significant difference between male and female hand-reared animals confirms the findings of Nissen and Riesen (1945). However, the full versus reduced model approach does show that tooth emergence in males proceeds at a significantly faster rate than in females among mother-reared animals at PFA, and this finding is consistent with a clear trend shown by the jackknife results. The full versus reduced model also reveals that PFA hand-reared females are significantly advanced over their mother-reared peers, a tendency similarly exhibited by the jackknife analysis. This tendency is not indicated for BA over the 0–24 month age range by either the jackknife or the full versus reduced model analysis. However, it is interesting to note that the trend in favor of the hand-reared females is clear and consistent throughout almost the entire age range for the PFA animals, whereas for BA the curves cross at the age of 8 months; up to that age the mother-reared animals are in the lead, and after 8 months the hand-reared are ahead, as they are at PFA.

Since a possible effect of rearing status on tooth emergence is indicated by our results, we suggest that curves for mother-reared animals in our sample may be of particular use in the assessment of tooth eruption status in fossil hominid specimens. Data from mother-reared captive animals are likely to be more directly relevant to conditions in the wild than data for hand-reared or for mixed samples of hand-reared and mother-reared captive animals.

CONCLUSIONS

There is variability in chimpanzee growth and development rates that has not been shown in previous studies. The earlier studies have been restricted almost entirely to single colonies of hand-reared animals and have examined differences only between

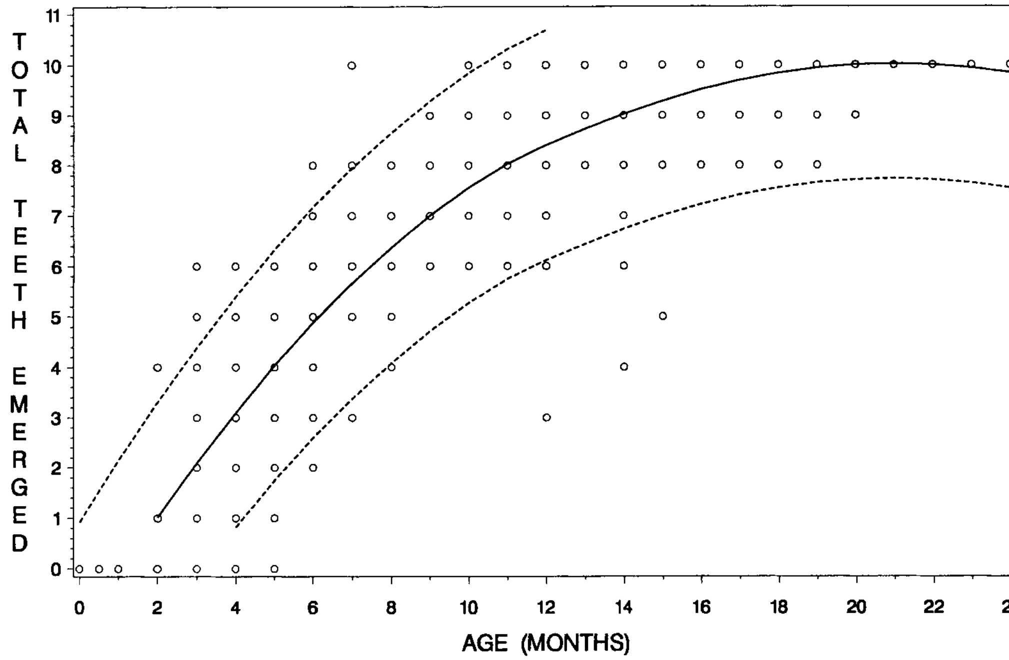

Fig. 6. Total dental emergence score versus age for the full sample. LOWESS fit and 95% prediction band.

sexes. We have found that rates of weight gain, and to some extent hand/wrist maturation and tooth emergence, all may be affected by sex and by some aspects of the circumstances under which they are raised.

The curves generated by the LOWESS method in our study therefore are useful in providing norms and estimates of variability for specific sex/rearing/colony groups within a large sample of chimpanzees from a variety of environments, which may serve as reference sources both for the assessment of developmental status for individual captive chimpanzees, and as standards for the assessment of deciduous dental status in fossil hominids.

Comparison of results from two approaches to the analysis of differences between pairs of curves for colony/rearing/sex groups within our sample indicates that there are clear patterns in growth and development variability. It is expected that the significance of differences already discerned among these groups will increase as sample size for our study increases and as statistical models are developed which are more suitable to the analysis of opportunistically-obtained mixed longitudinal data.

Evidence in this study for a possible effect of rearing on tooth emergence has implications for the application of data from living captive chimpanzees to estimation of tooth emergence status in fossil specimens. It is suggested that our tooth emergence curves for mother-reared captive chimpanzees may be more applicable to this purpose than curves generated from data on hand-reared captive animals.

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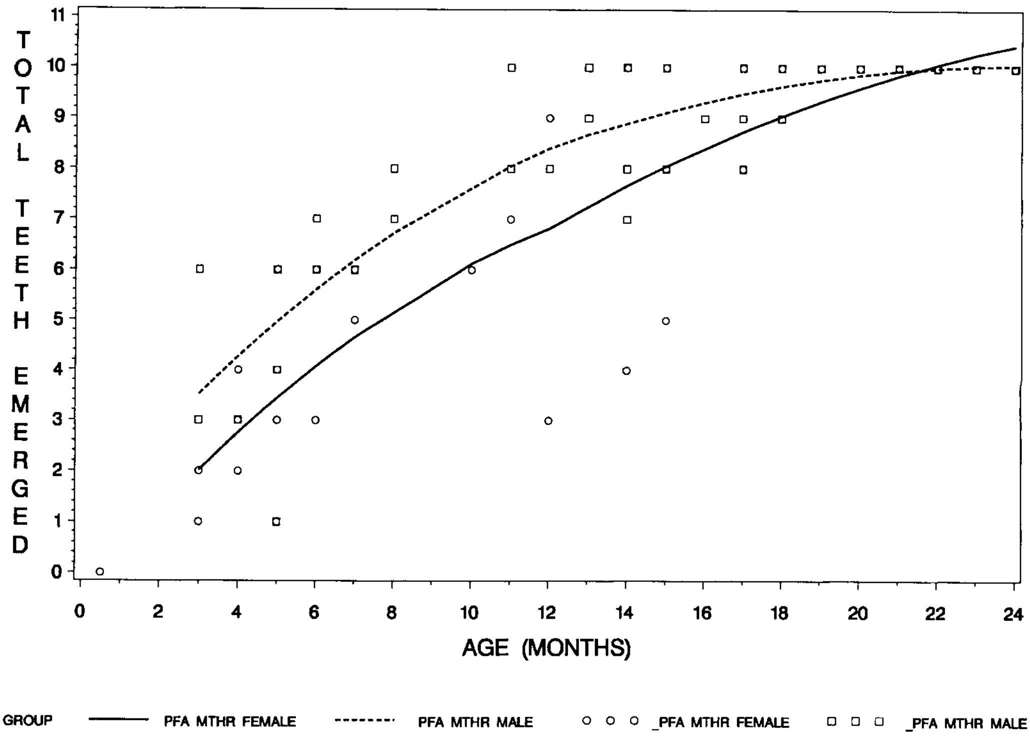

Fig. 7. Comparison of sexes in tooth emergence versus age: PFA mother-reared females and males. Comparison of LOWESS fits.

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APPENDIX. Results of comparison of LOWESS curves for weight, maturation and tooth emergence (α = 0.10) among colonies and rearing/sex groups, using the full versus reduced model approach

			P value		
Comparison	Group 1	Group 2	Weight	Maturation	Dental
Colonies	BA HF	PFA HF	0.0061		0.6652
	BA HF	WS HF	0*		0.6385
	BA HM	PFA HM	0*		0.2525
	BA HM	WS HM	0.0001*		0.1115
	BA MF	PFA MF	0*		0.1139
	BA MM	PFA MM	0.0103		0.9199
	PFA HF	WS HF	0.0233	0.0002*	0.6775
	PFA HM	WS HM	0.0117	0.0306	0.7183
Rearing groups	BA HF	BA MF	0*		0.8879
	BA HM	BA MM	0*		0.5173
	PFA HF	PFA MF	0*	0.0306	0.0021*
	PFA HM	PFA MM	0.0113	0.0167	0.1073
Sexes	BA HF	BA HM	0.0035*		0.3173
	BA MF	BA MM	0.5016		0.3727
	PFA HF	PFA HM	0.2626	0.1541	0.9436
	PFA MF	PFA MM	0.139	0.1279	0.0023*
	WS HF	WS HM	0.0005*	0*	0.7602

*Significant (overall α = .10 for each variable; individual α level using Bonferroni's method = .10/17 = .0059 for weight and dental values and .10/8 = .0125 for maturation values).